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Contents

Summary

The visual system achieves a tremendous amount of processing as soon as we set our eyes on a new object. In fact, numerous processes are active already *before* our eyes reach the object. The following thesis explores the spatio-temporal properties of three such processes: (1) attentional enhancement and saccadic suppression that accompany saccade generation to target; (2) attentional selection of the target in a visual-search task; (3) the timecourse of target detection accuracy under object-substitution masking. We monitored these events using a combination of human electrophysiology (EEG), eye tracking (ET) and behavioral psychophysics. In Study 1, we investigated how the neural representation of a visual stimulus is affected by its temporal proximity to the saccade onset. Specifically, we monitored for evidence of attentional enhancement and saccadic suppression across a distribution of saccadic reaction times. We show that stimuli immediately preceding a saccade show strongest effects of attentional enhancement and saccadic suppression. In Study 2, we used the reverse approach: based on stimulus visibility, we measured how quickly and accurately a saccade to target will be generated. Using object-substitution masking to reduce stimulus visibility, we analyzed the relationship between saccadic reaction times and the response accuracy. Additionally, we monitored the EEG for neural markers of attentional selection, such as the negative, posterior-contralateral deflection at 200 ms (N2pc), and collected behavioral ratings of subjective visibility of the target. We found that fast saccadic responses escaped the effects of masking and resulted in higher response accuracy as well as higher ratings of subjective awareness. This indicates that visual information is available already at early processing stages and can produce correct responses and a conscious awareness of the target. In study 3, we replicated this finding using manual responses. Discovering a similar accuracy timecourse in a different modality allowed us to rule out saccade-specific mechanisms, such as saccadic suppression and shift of the retinal image, as a potential confound in Study 2. In addition to their theoretical impact, all studies make a methodological contribution to EEG-eye movement research. Study 1 details how to remove large-scale saccadic artifacts from EEG data and describes an innovative method to compose a matched surrogate dataset. Study 2 employs the horizontal electrooculogram as a reference for precise saccade detection and artifact rejection. Finally, all three studies make use of surrogate data, either recorded separately as control conditions or bootstrapped from real data. In sum, this work uses multiple approaches to describe the dynamics of visual perisaccadic perception and offers solutions for future studies in this field.

Zusammenfassung

Das visuelle System erreicht enorme Verarbeitungsgeschwindigkeiten, sobald wir unsere Augen auf ein neues Objekt richten. Tatsächlich sind bereits zahlreiche Prozesse aktiv, bevor unser Blick das neue Objekt überhaupt erreicht hat. In der folgenden Doktorarbeit werden die räumlichen und zeitlichen Eigenschaften drei solcher Prozesse erforscht: (1) aufmerksamkeitsbedingte Steigerung der neuronalen Aktivierungen sowie sakkadische Suppression, die eine Augenbewegung zum Zielobjekt begleiten; (2) aufmerksamkeitsbasierte Selektion des Zielobjekts bei einer visuellen Suchaufgabe; und (3) die zeitliche Entwicklung der Antwortgenauigkeit in einer Zielreizdetektionsaufgabe bei der Objekt-Substitutionsmaskierung. Wir untersuchten diese Prozesse mit einer Kombination aus humaner Elektroenzephalografie (EEG), eye tracking (ET) und psychophysischen Verhaltensmessungen. In der ersten Studie untersuchten wir, wie die neuronale Repräsentation eines einfachen visuellen Reizes von seiner zeitlichen Nähe zum Beginn einer Sakkade beeinflusst wird. Insbesondere haben wir, mit Hilfe einer breitgefächerten Verteilung von sakkadischen Reaktionszeiten, nach Beweisen für eine aufmerksamkeitsbedingte Steigerung neuronaler Aktivität und nach sakkadischer Suppression im EEG gesucht. Unsere Daten weisen darauf hin, dass Reize, die unmittelbar vor einer Sakkade präsentiert werden, am meisten durch Aufmerksamkeitsprozesse verstärkt werden können und durch post-sakkadische Suppression geprägt sind. In der zweiten Studie verfolgten wir einen gegensätzlichen Ansatz: Abhängig von der Sichtbarkeit des visuellen Reizes, erfassten wir wie schnell und mit welcher Genauigkeit eine Sakkade zum Zielreiz ausgeführt wurde. Durch die Objekt-Substitutionsmaskierung wurde die Sichtbarkeit des Zielreizes verringert, und wir analysierten den Zusammenhang zwischen den sakkadischen Reaktionszeiten und ihrer Antwortgenauigkeit. Zusätzlich untersuchten wir das EEG auf neuronale Marker (wie z.B. die N2pc, ein neuronales Merkmal der Aufmerksamkeitslenkung zum Zielreiz), und erfassten subjektive Bewertungen der Wahrnehmbarkeit des Zielreizes. Wir stellten fest, dass schnelle Sakkaden dem Maskierungseffekt entgingen und zu einer höheren Antwortgenauigkeit sowie zu einer höheren subjektiven Wahrnehmbarkeit des Zielreizes führen. Dies deutet darauf hin, dass visuelle Informationen bereits in frühen Verarbeitungsstadien verfügbar sind und zu einer bewussten Wahrnehmung bzw. zu einer korrekten Detektion des Stimulus führen können. In der dritten Studie replizierten wir diesen Befund für manuelle Antworten anstelle von Augenbewegungen. Dies erlaubte uns auszuschließen, dass sakkaden-spezifische Mechanismen, wie sakkadische Suppression und die retinale Bildverschiebung, die Ergebnisse von Studie 2 verfälscht haben könnten. Zusätzlich zu ihrer theoretischen Bedeutung liefern alle drei Studien einen methodischen Beitrag zum Forschungsgebiet der EEG-Augenbewegung. Studie 1 zeigt wie großflächige, sakkadische Artefakte aus dem EEG entfernt werden können und beschreibt eine innovative Methode zur Erstellung eines künstlichen Vergleichsdatensatzes, welcher genutzt

werden kann, um sakkadische Einflüsse in den EEG Testdaten auszuschließen. Studie 2 nutzt das horizontale Elektrooculogram (HEOG) als Referenz für präzise Sakkadendetektion und Artefaktentfernung. In allen drei Studien werden Ersatzdaten verwendet, die entweder als Kontrollbedingungen aufgezeichnet wurden oder aus echten Daten berechnet wurden. Zusammenfassend werden in dieser Arbeit verschiedene Ansätze dargestellt und verwendet, um die Dynamiken visueller Wahrnehmung in dem peri-sakkadischen Zeitraum zu beschreiben, und diese Arbeit bietet zusätzlich Lösungen von Problemen, welche in zukünftigen Studien verwendet werden können.

List of original articles

This dissertation is based on the following original research articles:

Study 1

Kovalenko LY, Busch NA. (2016). Probing the dynamics of perisaccadic vision with EEG. *Neuropsychologia*, 85, 337–348.
doi:10.1016/j.neuropsychologia.2015.12.012

Study 2

Crouzet SM, Kovalenko LY, del Pin SH, Overgaard M, Busch NA. (under review in *Journal of Cognitive Neuroscience*). The early feedforward sweep allows for selective behavior, shifts of attention and conscious visual experience.

Study 3

Kovalenko LY, Crouzet SM, Busch NA. (submitted to *Frontiers Human Neuroscience*). The fastest behavioral responses can escape object substitution masking independent of the effector.

Abbreviations and key terms

EEG	Electroencephalography
ET	Eye tracking
ERP	Event-related potential
ERL	Event-related lateralization
VEP	Visual evoked potential
SOA	Stimulus onset asynchrony
(S)RT	(saccadic) reaction time
N2pc	negative deflection at 200 ms with posterior-contralateral topography
OSM	Object substitution masking
ICA	Independent component analysis
HEOG	Horizontal electro-oculogram
V1	Primary visual cortex

1 Introduction

Vision is the primary sense on which we rely to perceive and interact with our environment. Although our subjective visual experience is continuous and effortless, a great deal of complex processing takes place between "looking" and "seeing." This thesis will focus on the temporal properties of three physiological events that guide our visual experience from "looking" to "seeing": making an eye movement to a target, perceiving and/or becoming aware of the target, and responding to it. We explore these events at three physiological levels: automatic and unconscious (Study 1), behavioral (Studies 2 and 3), and cognitive (Study 2).

First, I will discuss the deployment of spatial attention to targets of voluntary eye movements (saccades). Although this deployment occurs automatically and remains unconscious, it affects the underlying neural signal (see Section 2). In Study 1, we investigated how the neural representation of a simple visual stimulus was affected by its temporal proximity to the saccade onset. Using a distribution of saccadic reaction times, we identified the correlates of attentional enhancement and saccadic suppression in the human EEG.

Second, we inspect the minimal amount of time that is required to register a target. We explored this question in the framework of the object substitution model (Di Lollo et al., 2000; Francis, 2007), which is thought to selectively disrupt the later stages of stimulus processing and interfere with conscious perception (see Section 3). In Study 2, we manipulated the visibility of the target using object-substitution masking (OSM) and measured the speed and accuracy of saccadic responses to it. We obtained a behavioral time-course for accurate detection of the stimulus and established how it correlates with the subjective ratings of stimulus awareness as well as with neural markers of attentional selection. We believe that our findings support and inform the theories of visual perception that link OSM to selective disruption of reentrant processing.

Finally, in Study 3 we explored how the final stage, responding to a target, varies across two different response modalities, saccadic and manual. We replicated the behavioral component of Study 2 and established that both saccadic and manual responses produce a similar accuracy time-course (see Section 4.3).

In sum, these experiments inspect the intersection of vision physiology and perception at three different stages: making an eye movement, processing visual input, and responding to a stimulus. In the following chapters, I will provide theoretical and methodological background, along with a critical discussion of results, separately for each stage.

2 Moving the eyes: attention and visibility dynamics around saccade onset

We are constantly moving our eyes to explore the visual environment. In fact, eye movements (saccades) are the most frequent movement in the human body. As not all regions of the retina are equally sensitive, saccades are a necessary component of vision that actively aligns the most sensitive region of the retina, the fovea, with the object of interest. The fovea itself covers about 2° of the visual field; hence, it must be shifted several times across the visual field to scope it in its entirety. Interestingly, eye movements are as instrumental for vision as they are disruptive; in fact, each saccade entails perceptual costs, such as an interruption of clear vision that results from blurring of the retinal image during saccades, and displacement of the retinal image from one fixation to the next (see Sommer and Wurtz, 2008, for a review). To counteract this blur and sharpen the perception of the new object, multiple neural processes are at work before and after each saccade onset. This section will focus on two such mechanisms, pre-saccadic shifts of attention and saccadic suppression.

Pre-saccadic shifts of spatial attention are an important example of the interplay between saccades and cognition: stimuli appearing at the target location during the saccade preparation are associated with shorter reaction times, improved discrimination at the saccade target and stronger physiological responses (Kowler et al., 1995; Deubel and Schneider, 1996; Moore and Fallah, 2001; Wauschkuhn et al., 1998). While the shift of attention enhances visual sensitivity to the future target, the saccadic suppression, inhibits the sensitivity to non-target objects in order to minimize the retinal blur (Burr et al., 1994; Volkmann et al., 1978; Diamond et al., 2000; Ross et al., 2001; Bremmer et al., 2009). The goal of Study 1 was to identify the correlates of these two processes in the human EEG and specify the time-windows when they are most pronounced.

2.1 Addressing methodological challenges: artifact removal and validation

Although perisaccadic perception has been the focus of numerous behavioral and animal studies, research employing human electrophysiology is very limited. In fact, this is a major research gap: EEG yields a continuous and temporally accurate record of neural activity across the whole scalp. Thus, it lends itself as the method of choice for capturing both the temporal and, to a certain extent, the spatial aspect of perisaccadic events. However, due to substantial methodological difficulties with removing large-scale saccadic artifacts from the neural data, only a few attempts have been made to explore the perisaccadic processes with EEG (Parks and Corballis, 2008, 2010; Wauschkuhn et al., 1998). Therefore, the methodological goal of the Study 1 was to establish a protocol that of-

fers precise control over the saccadic artifact. Recent methodological developments have greatly facilitated the procedure for co-registering the EEG with eye tracking (Dimigen et al., 2011), subsequent saccade detection (Engbert and Mergenthaler, 2006), and artifact removal (Plöchl et al., 2012). Building on these recent advances, Study 1 devised a set of solutions for dealing with saccadic artifacts that reside in close temporal proximity to the stimulus, such as removing the artifacts using ICA and computing a matched surrogate dataset to control for any saccadic and computational artifacts and validate in the experimental data.

2.2 Study 1: Empirical objectives

The empirical goal of Study 1 was to identify the spatio-temporal dynamics of automatic deployment of attention and saccadic suppression in the continuous human EEG. To achieve this, we measured the neural response to two simple checkerboard stimuli (probes) that were briefly flashed either in the same hemifield as the saccade target or in the opposite hemifield. For both spatial layouts, we recorded a distribution of probe-saccade stimulus onset asynchronies (SOA), which allowed us to monitor how the promixity of the impending saccade affects the neural representation of the stimulus.

It should be noted that behavioral studies investigating spatial allocation of attention with eye movements typically use different types of cues, for example, one to indicate the saccade direction and the other to indicate and/or manipulate the expected location of the probe stimulus. This allows to dissociate performance benefits arising from saccade execution vs. those of expecting a target at a pre-cued location (Posner, 1980; Shepherd et al., 1986; Deubel, 2008; Meyberg et al., 2015). We would like to clarify in advance that this was not the intent of our study. In our paradigm, 100%-valid symbolic cues were used only to indicate the saccade direction and were not predictive of the probe location. Likewise, our paradigm did not employ a behavioral task that could extrinsically manipulate the deployment of attention. Thus, our measurement captures the automatic processes that are triggered by saccade generation to target and presents a physiological reference for future studies that intend to combine visual stimuli and saccades the EEG.

3 Target perception: What object substitution masking can reveal about visual feedback processing

Study 1 characterized the time-course of physiological processes that automatically accompany typical saccadic behavior. In Study 2, we reversed the approach: we observed the accuracy of saccadic responses resulting from selective interference with the processes that underlie target perception. Using object substitution masking (OSM) to reduce target visibility, we measured the accuracy time-course for fast vs. slow saccadic responses. While the perceptual and neural mechanisms necessary for visual awareness remain a matter of debate, several theories assume that reentrant processing plays a key role in the formation of perception and awareness (Dehaene and Changeux, 2011; Lamme, 2006; Overgaard and Mogensen, 2014; Tononi and Koch, 2015). Visual brain areas are heavily interconnected, and most of these connections are reciprocal. The term "reentrant" or "recurrent processing" refers to the flow of information along these reciprocal connections, whereby the information arrives at the same neuronal assembly multiple times: once during the initial feedforward sweep starting at the primary visual cortex, V1, and later through feedback connections from higher brain areas with larger and more complex receptive fields. Thus, the recurrent information is usually thought of as more elaborate or complex. This hypothesis is supported by a number of physiological and psychophysical findings.

In psychophysics, the interplay between feedforward and reentrant processing has been studied using visual masking (Bachmann, 2006; Breitmeyer and Ogmen, 2006). Specifically, object substitution masking (OSM), stands as particularly relevant to that aim. OSM occurs when a briefly presented target in a search array is surrounded by small dots that remain visible after the target disappears (Di Lollo et al., 2000). This delayed offset strongly reduces target visibility. Thus, unlike pattern masking or meta-contrast masking, the masking effect results from the delayed mask *offset* rather than its delayed *onset*. Therefore, OSM is also referred to as common onset masking. Di Lollo et al. (2000) proposed that the representation of the target-plus-mask initially proceeds undisturbed through the feedforward sweep, and that OSM occurs when a mismatch arises between the reentrant signal representing target-plus-mask and the ongoing activity at the lower level representing the mask alone. This mismatch results in the replacement of the target-plus-mask representation with the mask-alone representation. While it is still debated whether the performance impairment under OSM is due specifically to object substitution, there is some agreement that OSM affects some later processes beyond the initial feedforward signal (Francis and Hermens, 2002; Põder, 2013; Goodhew et al., 2013; Di Lollo, 2014). Thus, in contrast to other forms of backward masking, OSM has been claimed to selectively disrupt reentrant processing while leaving the initial feedforward sweep intact (Di Lollo et al., 2000; Enns, 2004).

3.1 Behavioral level: Establishing the time-course of object detection under masking

The hypothesis that OSM is associated with an intact feedforward sweep, while later recurrent processing is disrupted predicts a specific temporal pattern of task performance: the accuracy of behavioral responses should strongly depend on the time when these response are initiated. Thus, particularly fast responses, already initiated during the first feedforward sweep, should be mostly unaffected by OSM, while the perceptual impairment should affect mostly slower responses.

To test this hypothesis, we recently established a masking paradigm in which two critical items (one target and one lure) are embedded in a search array and surrounded by four-dot masks (Crouzet et al., 2014). Unlike previous OSM studies that emphasized response accuracy over speed, we asked observers to make a saccade as fast as possible towards the target item. We found that OSM and backward masking impaired performance predominantly for slower saccades, while the fastest saccades under masking were as accurate as comparably fast saccades without a mask. This sparing of the fastest saccades cannot be explained by a generic, time-independent performance impairment. By contrast, a simple reduction of stimulus contrast yielded a comparable reduction of response accuracy but was independent of response speed (Crouzet et al., 2014), demonstrating that a general perceptual impairment affects all processing stages equally.

The objective of Study 2 was to extend this finding and explore what neural events are associated with the correct behavioral responses in the time-window where saccadic responses escaped masking. Hence, in addition to measuring behavioral responses, we recorded EEG which we inspected for electrophysiological correlates of attention shifts.

3.2 Neural level: Relating components of attentional selection to accuracy

Recently, a number of event-related potentials (ERP) studies have found that successfully masked targets still elicit a shift of spatial attention towards the target as indexed by the N2pc component of the ERP (Harris et al., 2013; Prime et al., 2011; Woodman, 2010; Woodman and Luck, 2003). The N2pc (N2-posterior-contralateral) is a negative-going deflection of the ERP at posterior channels contralateral to a relevant stimulus with an onset latency of approximately 200 ms. Taking at face value the hypothesis that OSM interferes mostly with later reentrant processing, these results suggest that the target detection and a subsequent shift of attention towards the target can be triggered based on the initial feedforward sweep, even if the mask disrupts reentrant processing. If that is indeed the case, correct *fast* saccadic responses under OSM should be accompanied by an N2pc. For responses under common offset, visual information is not overwritten by

the trailing mask, therefore N2pc should occur on both fast and slower correct trials.

3.3 Cognitive level: Dissociating target detection from target awareness

The final goal of Study 2 was to dissociate correct responses to the target from conscious awareness of it. According to the theory of object substitution masking, OSM should selectively disrupt reentrant processing which is believed to support visual awareness. Several studies have provided evidence that information processed during the feedforward sweep remains unconscious if reentrance is disrupted, e. g. by masking or TMS (Di Lollo et al., 2000; Silvanto et al., 2005; Lamme, 2006; Boehler et al., 2008). In fact, numerous studies have used OSM as a proxy for a selective disruption of reentrant processing. The reasoning is that if performance on a task is impaired by OSM, this task is assumed to require reentrant processing. By contrast, if performance is not impaired, it is assumed that this task is based on the unimpaired feedforward sweep (e.g. Ro et al., 2003; Bouvier and Treisman, 2010; Dux et al., 2010; Koivisto, 2012). For example, several studies have demonstrated that even when the target cannot be consciously identified under OSM, its low-level, unbound stimulus features can be detected (Chen and Treisman, 2009; Bouvier and Treisman, 2010), consistent with the notion that these processes do not require recurrent processing.

These reports indicate that, during the initial feedforward sweep, objects can be detected correctly in the absence of an accompanying subjective awareness. To test this possibility, after each trial the observers reported the targets' subjective visibility. We anticipated that fast trials, triggered during the initial fast forward sweep, will be accurate, but also associated with low subjective visibility.

3.4 Extending the paradigm into another modality and validating saccadic findings

In the original investigation, Crouzet et al. (2014) designed the paradigm using a saccadic choice task, because saccades to target stimuli can be particularly fast. For saccades, the earliest time at which correct responses outnumber errors can be as fast as 100–150 ms after stimulus onset (Kirchner and Thorpe, 2006; Crouzet et al., 2010), while a comparable precision with manual responses is only achieved starting at 250 ms (VanRullen and Koch, 2003). Thus, saccades were an ideal tool for investigating the time-course of accuracy over time, where the objective was to focus on the fast responses that may reflect the feedforward sweep.

However, we believe it is critically important to extend the saccade-specific findings and reasoning to another modality. In simple words, we have interpreted the finding reported

in Crouzet et al. (2014) as follows: fast saccades can escape masking because the effect of masking sets in at a time when the motor command has already been issued. If this interpretation is correct, then the benefit of responding fast should be independent of the effector, and fast manual responses should therefore demonstrate the same benefit.
Moreover, testing manual responses will allow us to rule out the involvement of two saccade-related mechanisms – saccadic suppression and the shift of retinal image – as potential confounds in our previous finding. Eye movements produce a substantial change in the visual input. First, visual input is known to be suppressed while the eyes are moving (Ross et al., 2001) and this suppression may truncate the effective duration of the trailing mask. Second, the shift of the retinal image causes a misalignment of target and mask in retinotopic coordinates. Given that the reentrant model of OSM assumes the trailing mask to interfere with the target at the same location, the retinal shift following saccades might render the mask ineffective. Thus, the consequence of the effect we previously observed might have been that fast saccades are unimpaired by masking not because they actually escaped the mask, but because they effectively eliminated the mask in the first place. Importantly, manual responses are not influenced by either of these effects. Thus, we will conduct the experiment using the same paradigm and analysis, but replace eye movements with button presses. If fast manual responses show, like saccadic responses, less impairment than slower manual responses, it is likely that this benefit is indeed due to a masking mechanism that affects only later stages of the visual processing cascade during reentrant processing.
The manual responses are expected to be generally slower than saccadic responses. For example, Bacon-Macé et al. (2007) compared saccadic and manual responses in a natural scene discrimination task and found that both minimal and median manual response times were delayed by approximately 150 ms compared to saccadic response times. However, the present experiment does not require that saccadic and manual responses be matched in terms of absolute response speed. Rather, we only assume that whatever processes are responsible will add a constant delay to the time required for the perceptual decision. We thus predict that manual responses whose speed approximates the minimal *manual* response time (i.e. the earliest latency at which correct manual responses outnumber incorrect manual responses) are unaffected by masking.

3.5 Studies 2-3: Empirical objectives and their theoretical implications

The object substitution model provides a theoretical framework, in which we can empirically test multiple aspects of visual perception.

- We will use fast behavioral responses to infer about the information carried along the feedforward sweep. At short RT, we should observe comparable accuracy per-

formance for both masked and common offset conditions; at longer latencies, performance under masking should be impaired, while performance under common offset should remain constant or improve. This finding would substantiate previous reports (Crouzet et al., 2014) and establish that detection of simple stimuli can be achieved by the feedforward processes only.

- We will complement behavioral responses with an EEG recording and analyze whether correct behavioral responses are accompanied by neural events, such as shifts of attention to the hemifield containing the target.

- We will collect ratings of subjective visibility. These will provide a parallel measurement, that may allow us to dissociate visual detection from visual awareness. Further findings at this intersection will inform the theory of object substitution masking, which predicts correct performance without a subjective awareness.

- We will replicate the behavioral component of this study using manual presses. This will not only substantiate our finding in a different domain, but also rule out saccade-specific mechanisms which could interfere with masking and thus pose a significant challenge to previous reports using saccades.

4 Results and discussion

4.1 Study 1: Identifying the time-course of perisaccadic enhancement and suppression in EEG

4.1.1 Study 1: Automatic deployment of attention to the target hemifield

In Study 1, we inspected perisaccadic perception using EEG. To achieve this, we presented a salient probe shortly before saccade onset and monitored the neural response to this probe. Specifically, we inspected how this response is shaped by the probe's spatial location relative to the saccade target as well as its temporal proximity to the saccade. We tested two spatial configurations of stimulus location and saccade direction: in the first, the probe appeared in the same hemifield as the saccade target, which we called the "prepared" (PREP) condition (see Figure 1, A, red boxes); in the other, target and stimulus appeared in the opposite hemifields, which we called the "unprepared" (UNPREP) condition (see Figure 1, A, blue boxes). As we recorded many trials from a broad range of saccade latencies, we were able conduct a single trial-analysis, sorted by probe-saccade SOAs; this gave us an insight into the temporal development of the neural response in two spatially different conditions. Additionally, we computed surrogate data that closely matched the real data (see Figure 1, B) as a novel approach for validating findings and controlling for computational artifacts.

We performed the first analysis in three steps. First, we inspected the lateralized neural response to probes. Since the probes were presented laterally, they were expected to evoke a neural response in the contralateral cortical hemisphere. To isolate signals specifically reflecting the probe-evoked neural response and to remove non-lateralized signals (e.g. response to the fixation cross), we analyzed EEG lateralization as the difference between channels contralateral vs. ipsilateral to the probe. Second, we performed a single-trial analysis to observe how the neural response changes with its temporal proximity to a saccade. We visualized the results in a series of ERP-images (Jung et al., 2001), applying a recent extension of the ERP-image method, where single trials are averaged across subjects to produce a "grand" ERP-image plot (Delorme et al., 2014). This additional step offered several advantages: it produced a more compact measure, averaged out unsystematic noise, and the resulting image was fit for statistical testing. Finally, to quantify the relationship between the strength of probe representation (voltage) and probe-saccade SOA, we correlated voltage with increasing probe-saccade-SOA across single-trials in the grand ERP-image using Spearman's correlation coefficient, *rho* over 1000 resamples. This analysis is sensitive to dynamic patterns in the data: flat segments indicate that the voltage is consistent across all saccadic latencies, whereas rising and falling trends indicate that the strength of the probe representation changes with respect to the saccadic latency. We established that the strength of the neural response to the probe changed with probe-

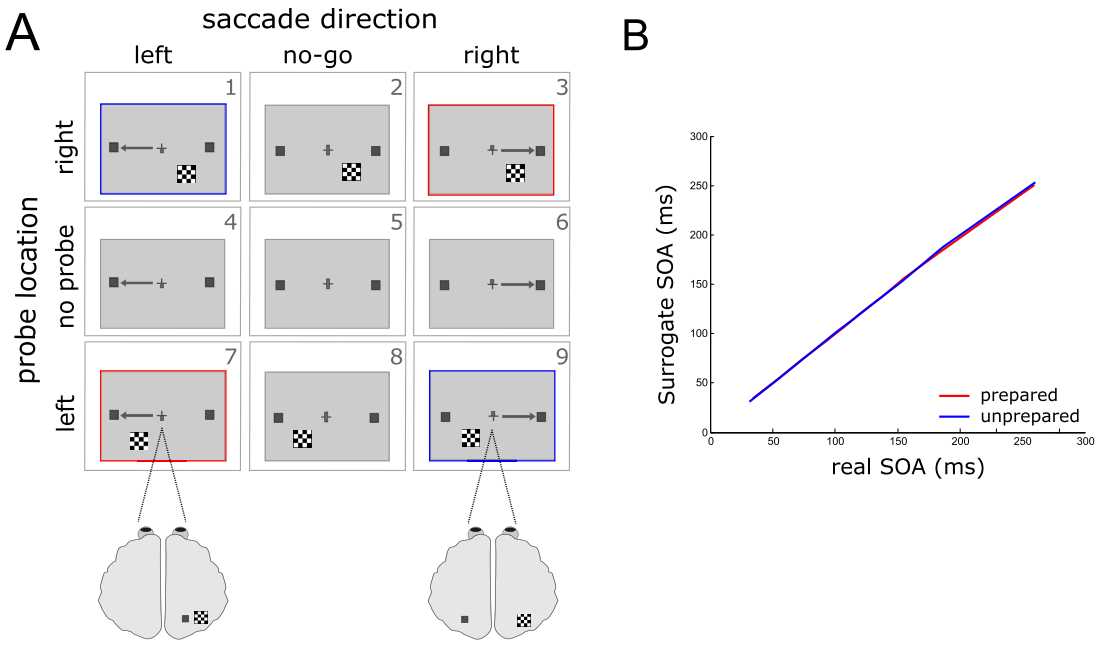

Figure 1: **Study 1: Experimental design**. **A** Experimental design and spatial configuration of stimuli. For experimental trials, probe and saccade target appeared either in the same (boxes 3 and 7, marked in red) or in different hemifields (boxes 1 and 9, blue). Insets below illustrate the retinotopic mapping for PREP (red) and UNPREP (blue) conditions. Unmarked boxes represent control conditions: probe-only (boxes 2 and 8), saccade-only (boxes 4 and 6), and cue-only (box 5), which were used to produce the surrogate dataset. **B** Direct comparison of binned reaction times in real conditions and their surrogate homologues. The probe-saccade SOAs align well for each condition and bin, indicating a close temporal match between real and surrogate data.

saccade SOA (see Figure 2). Moreover, we found that the direction of these correlations was different in PREP vs. UNPREP data (see Figure 3). In the PREP condition, we found strongest voltage at short SOAs, which receded towards longer SOAs. In the UNPREP data, we observed the opposite: voltage was weakest at short SOAs and increased at later saccades. We believe the first finding reflects specific deployment of spatial attention.

In our paradigm, there are two components that can deploy or capture attention: the saccade and the peripheral probe. It is well-established that making a saccade necessarily triggers the allocation of attention to the target location (Shepherd et al., 1986; Kowler et al., 1995; Hoffman and Subramaniam, 1995; Deubel and Schneider, 1996). Likewise, presenting a peripheral stimulus attracts attention. Previous studies found that making a saccade necessarily involved attentional allocation to the target position, which preceded the saccade. And further, this allocation was uneven: if the probe and saccade target were on the same side, the overall effect on RT was facilitatory; but, if they were on the opposite sides, the saccade target attracted attention stronger than the peripheral target. This competition dissipated at longer probe-saccade SOAs (between 140-300 ms). This pattern

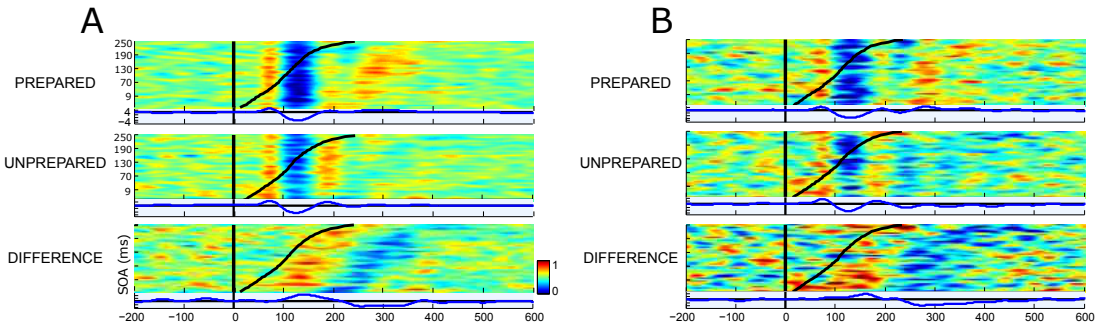

Figure 2: **Lateralization patterns for stimuli in prepared vs. unprepared hemifields**. **A**: Single-trial ERLs are sorted by increasing probe-saccade SOAs (shortest SOA at the bottom). PREP and UNPREP conditions show opposite trends: at the shortest latencies, the response is strongest in PREP and weakest in UNPREP. This pattern reverses at longer SOAs. The difference signal reveals an underlying lambda wave (saccadic VEP). **B**: surrogate data show a similar, but less consistent response pattern.

parallels our physiological findings – our probes appeared in the time-window where this competition of saccade target and the peripheral probe was found. The competition pattern itself is also apparent in our physiological findings as: we observe the facilitation for PREP, but not for UNPREP stimuli, where the saccade target is probably withdrawing attention from the probe. As we instructed our subjects to focus on making precise saccades and disregard the probe stimulus, our data do not show the same RT effect as Shepherd's: PREP stimuli are not followed by faster saccades; rather, we find that they produce bigger electrophysiological responses when compared to identical latencies of the UNPREP data or to surrogate homologues (see Figure 3).

Our pattern is also consistent with two well-established findings from the physiological literature. First, deploying attention to a stimulus produces an enhanced neural response. This has been observed both in single-cells (Moran and Desimone, 1985) and in the visual evoked potentials (Eimer, 1993; Hillyard and Anllo-Vento, 1998). Second, the enhanced response at the attended location is often accompanied by an attenuated response at the unattended location (Desimone and Duncan, 1995). We observe both effects in our data: for the fastest saccades (up to 100 ms), the PREP probes evoke the biggest voltage, while the UNPREP probes at identical latencies show a reduced voltage, likely reflecting the side from which attention is withdrawn. This trade-off is most pronounced at short probe-saccade SOAs. However, if the probe and the saccade are separated by an SOA of 100 ms or more, UNPREP probes also produce stronger responses, indicating that the competition is lifted, which is also consistent with Shepherd's behavioral time-course.

Finally, it is reasonable that the biggest difference between attended and unattended probes is found closest to the saccade onset. Behavioral findings of Deubel (2008) indicate that pre-saccadic attention shifts may occur within 50 to 150 ms. The pattern of our findings is consistent with this time course: at short SOAs (0–100 ms), there is probably

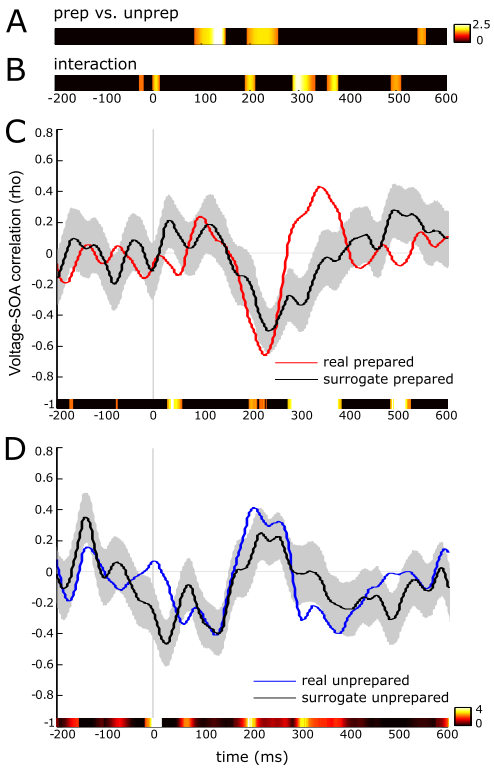

Figure 3: **Study 1: Correlation of voltage with probe-saccade SOA**. **A**: Heat map shows time-windows where PREP and UNPREP data are statistically different (main effect): 85–150 ms, 190–260 ms. **B**: Heat map shows the 2 x 2 interaction effect between condition (PREP vs. UNPREP) and data type (REAL vs. SURR), which was significant between 190–210 ms, 285–335 ms and 360–380 ms. **C, D**: correlation between voltage and probe-saccade SOA (Spearman's *rho*) for PREP (red) and UNPREP (blue) conditions against their respective surrogates (gray). Central line shows the median of the *rho* distribution, shaded regions represent the 95% confidence interval. Heat map at the bottom highlights the time-intervals, where real and surrogate are significantly different (hot colors represent $p < 0.05$, bright yellow – $p < 0.001$). For PREP, these time-windows were between 195–210 ms and 290–385 ms. For UNPREP: 190–215 ms and 290–320 ms.

enough time just for one attentional shift. Thus, in the PREP trials, both probe and saccade target can be probably attended in a single attention shift, whereas in the UNPREP trial, attention shifts towards the saccade target, bypassing the peripheral probe. Longer SOAs potentially allow enough time for two attentional shifts; hence, during the delay participants may attend covertly to the peripheral probe and then make a saccade to the target.

The parallels between our paradigm and previous attentional findings allow us to conclude that the dynamics we observe in the ERP-image reflect the competition for spatial attention. Further, our physiological observations complement the behavioral findings, illustrating the allocation of spatial attention to the probe. Finally, using the saccadic RT as a point of reference, we visualize a fine-grained time-course of attentional deployment.

The other difference we identified between PREP and UNPREP data was a late positivity that was specific to real PREP data. The saccade-locked pattern suggests that this activity may represent the late phase of the lambda wave. The early lambda component which is typically found as soon as 80 ms after saccade offset and is believed to represent the visual potential evoked at re-fixation (Yagi, 1979; Thickbroom et al., 1991; Kazai and Yagi, 2003). Additionally, it has been shown that the late lambda components are sensitive to stimulus properties, attentional load and arousal (Yagi, 1981; Marton et al., 1983; Nagai et al., 2001). In particular, "oddball" stimuli that appear unpredictably or irregularly lead to stronger post-saccadic "detection positivity" (Cooper et al., 1977; Marton et al., 1983; Kamienkowski et al., 2012). Several studies have implicated this late positivity in the processing of visual information, which resumed after the saccade, as well as related it to the P300 observed at fixations (Marton et al., 1983; Dandekar et al., 2012). The late effect we observe in the PREP data – where the probe appears unpredictably next to the saccade target – is consistent with the nature, the timecourse, and the occipital topography of the previously described "detection positivity" effect. Therefore, this late finding may inform us about the post-saccadic processing of the attended pre-saccadic stimulus.

4.1.2 Study 1: Saccade-induced reduction of the neural signal

Our second analysis was conducted using unlateralized ERP data. As in the previous analysis, we produced a grand ERP-image and analyzed the correlation of voltage and probe-saccade-SOA over 1000 resamples. We observed that real data evoked an overall weaker response compared to surrogate data. On closer inspection of the SOA-sorted data, we found that this effect was specific to short SOAs, where surrogate data showed excess positive voltage. We believe that this second points to inhibitive probe-saccade interactions that occur regardless of the spatial configuration of stimuli.

When comparing real and surrogate data in the unlateralized analysis, we found that the surrogate data produced stronger responses in the late time-window. In the ERP-

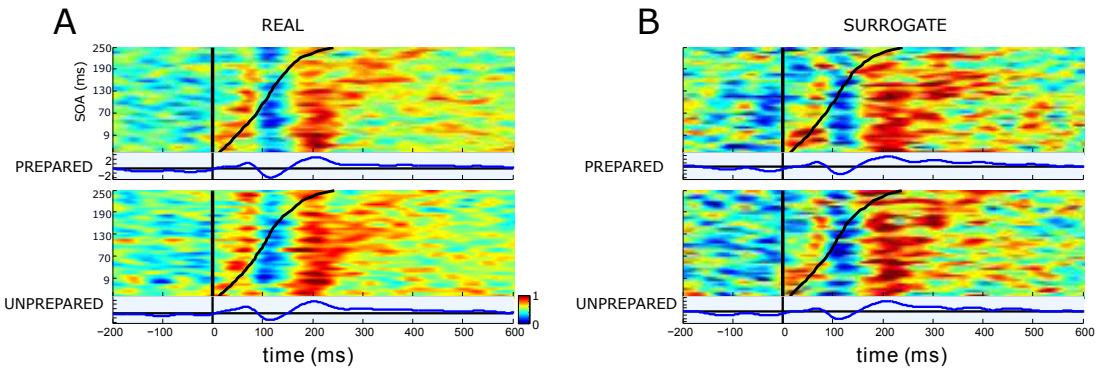

Figure 4: **Real data show reduced responses A** Single-trial ERP data are sorted by increasing probe-saccade SOAs (shortest SOA at the bottom). PREP and UNPREP conditions both show an early positive activity between 0–70 ms, followed by a probe-locked negativity between 95–150 ms and a saccade-locked positive sweep that likely reflects the lambda-wave. **B** Surrogate sets show more positive activation for short SOAs.

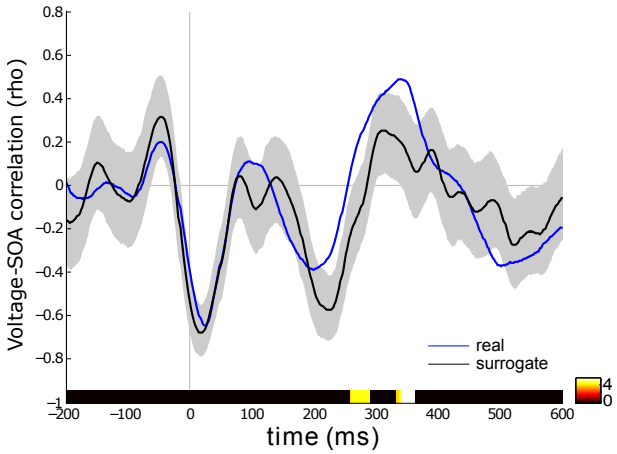

Figure 5: **Study 1: Real data show reduced responses**. Correlation between voltage and probe-saccade SOA for combined real (blue trace) and surrogate (black trace) conditions. Solid traces show the median of the *rho* distribution, the shaded region represents a 95% confidence interval for the surrogate data. Color bars at the bottom highlight time-intervals where real and surrogate are significantly different: between 260–290 ms and 330–360 ms, p = 0.001 (FDR-threshold of $p < 0.05$).

image, this pattern was localized at short probe-saccade SOAs and was confirmed in the resampled correlation analysis (see Figure 5). This finding indicates that adding up the individual neural representations of probe and saccade does not produce the same response as perceiving these stimuli on the same trial. This in turn implies that real data contain complex interactions between the probe and the impending saccade that do not occur in the surrogate data. Further, this difference seems to reflect a saccade-evoked modulation that does not depend on the spatial layout of the stimuli. In other words, the effect we see here is different from the "attentional" finding, which was specific to the spatial configuration of stimuli. The reduction suggests that the nature of this interaction is inhibitive – the probe representation seems partially "erased" or suppressed by the impending saccade.

A candidate mechanism that could explain the reduction in voltage is the saccadic suppression, which is a transient reduction in visual sensitivity that counteracts the blurring of the retinal image during eye movements (see Ross et al., 2001, for a review). Our probe stimulus was a low-spatial-frequency, black-and-white checkerboard that would normally stimulate the magnocellular stream, a pathway that is selectively inhibited under saccadic suppression (Burr et al., 1994). Psychophysics indicate that suppression occurs within a specific time window: it sets in at around 50 ms before the saccade onset and outlasts saccades by about 50 ms (Diamond et al., 2000). Electrophysiological recordings from motion-sensitive areas of the monkey cortex report a reduced population firing response between the onset of the saccade and up to 150 ms afterwards (Bremmer et al., 2009). Further, electrocorticographic recordings showed saccade-related gamma attenuation that persisted as long as 250 ms after the saccade offset (Uematsu et al., 2013). The onset of our inhibition effect is consistent with the late reduction of activity; however, we do not observe the pre-saccadic or early perisaccadic reduction that is typically reported in the context of the saccadic suppression. While it is surprising that we only see the late reduction effect, there are possible explanations. First, physiological recordings in monkeys sample the behavior of a very localized subset of neurons, whereas our ERP reflects an average across multiple sources; hence, the low spatial resolution possibly obscures local effects. Indeed Uematsu et al. (2013) investigated perisaccadic occipital activity using a surgically implanted intracortical electrode grid. Their high-resolution recording (inter-electrode distance was 10 mm) showed that human occipital cortices exert saccadic suppression differentially: the attenuation is strongest in the polar occipital region and weakest in the medial occipital region. Moreover, in their data, these regions produced saccade-locked ERPs of opposite polarities: negative peaks were recorded from polar and lateral occipital regions, whereas the medial region produced positive ERP peaks. Our ERPs reflect an average over six occipital electrodes, located relatively far apart from each other. At this spatial resolution, fine-grained local differences cannot be detected. Instead, the opposite polarities are averaged together. This averaging may explain why

we do not observe a pronounced early effect of saccadic suppression.

4.1.3 Future directions and suggestions

Including a separate task to test attention Co-registering the eye track with our EEG has provided a precise record of the saccadic reaction times, which in turn has optimized artifact removal and helped compute an accurate surrogate. Now that the paradigm allows to obtain accurate and reproducible data, it can also be easily expanded, for example to include a behavioral task, e.g. detection or orientation discrimination, that can be used to quantify attentional enhancement as well as correlate the time course of the attentional enhancement with the neural events we observe in the EEG. Such a task would make it easier to relate future EEG findings to the existing body of behavioral literature on attention and help resolve inconsistencies. For example, previous behavioral studies indicate that we should observe faster RTs on attended trials. We do not observe such an effect. However, it should be noted that during the pre-processing, we have purposely removed extra fast trials on which the saccade preceded the probe. This step was necessary to optimize the ERP analysis; however, it is possible that by truncating the RT distribution we have also eliminated the trials that would otherwise point to the RT benefit. Having a separate behavioral performance task would resolve this limitation: trials that cannot be included in the ERP analysis would still contribute the behavioral information, such as the RT and the corresponding performance, that would allow to quantify any attentional enhancement.

Decomposing ERP into stimulus- and saccade-locked components Our ERP-image analysis revealed response patterns that are time-locked to the probe and the saccade. At short probe-saccade SOAs, these patterns overlap, making it difficult to establish the nature of the effect. In particular, in our inhibition finding, we currently cannot isolate with certainty the component that is being inhibited – the response to the probe or the saccade-locked lambda wave. Future studies should include an additional analysis that dissociates the ERP signal, for example using the RIDE method (Ouyang et al., 2011, 2014). Using a response variable, such as saccadic RT, this method decomposes the averaged ERP into stimulus-locked, response-locked and residual components. Dissociating the ERP into separate probe- and saccade-locked components would be quite useful, as it would allow to resolve the overlapping activity at short SOAs. Further, it would allow to compare the strength of these signals quantitatively, for example, by adding up the voltages corresponding to the probe-response and the lambda-wave at different latencies. Based on our findings, we predict that the sum of the probe-response and the lambda-wave will be larger at long SOAs vs. short SOAs, as we do not expect to observe any inhibition of the probe-signal at long SOAs.

Controlling noise in the surrogate The surrogate data have been a helpful reference point in our analysis. Using such data, however, is tied to an important limitation: they represent the result of adding and subtracting three subsets of separately recorded data; therefore, the surrogate data are inherently noisier. It is difficult to diminish this noise further in the surrogate data using ICA. One potential method to make the two datasets even more comparable is to run a computation that injects noise into the real data. If the difference observed between real and surrogate data survives this manipulation, the noise can be ruled out as a confound in this experiment.

4.1.4 Study 1: Summary of results

Study 1 successfully identified perisaccadic activity related to automatic allocation of spatial attention and to perisaccadic suppression. Further, it identified evidence of stimulus processing that resumes after saccadic offset. We employed recent methodological advances to co-register EEG with eye tracking and remove strong ocular artifacts. By computing a matched surrogate dataset, we were able to control for any saccadic and computational artifacts and validate the effects in the real data.

Complementing previous behavioral evidence, our physiological findings illustrate the allocation of spatial attention to the probe, using the saccadic RT as a point of reference, relative to which the dynamics of voltage enhancement or attenuation are observed. Based on these dynamics, stimuli located in the same hemifield as the saccade target and preceding the saccade onset by less than 100 ms show an enhanced neural response, compared to the stimuli in the opposite hemifield. This pattern reverses at longer delays between stimulus and saccade. Between 280–320 ms, we also observed a voltage attenuation in the real data that suggest inhibitive interactions between probe and saccade.

In the future, our experimental design can be expanded to investigate complex perisaccadic processes, such as attentional selection, saccadic suppression and perisaccadic remapping.

4.2 Study 2: Time-course of accuracy and awareness under object substitution masking

4.2.1 Study 2: Dissociating accuracy from awareness

Numerous studies have demonstrated that various forms of masking cause an impairment of visual performance and have studied how mask properties (e.g. spatial arrangement or timing) affect this impairment (see Goodhew et al., 2013, for a review). By contrast, much less is known about how the masking effect develops over time. In this study, we tested the hypothesis that object substitution masking leaves the initial feedforward sweep intact, allowing for target detection and shifts of spatial attention, but interferes during a later processing stage, presumably during reentrant processing. Observers were to detect target stimuli masked by a four-dot common-onset mask—a procedure called object substitution masking (Di Lollo et al., 2000)— and to make a saccade as fast as possible to the target's location (Crouzet et al., 2014) (see Figure 6). As expected, masking impaired performance in the saccadic choice task (Fig. 7A) and reduced objective performance and subjective awareness (Fig. 7B and C).

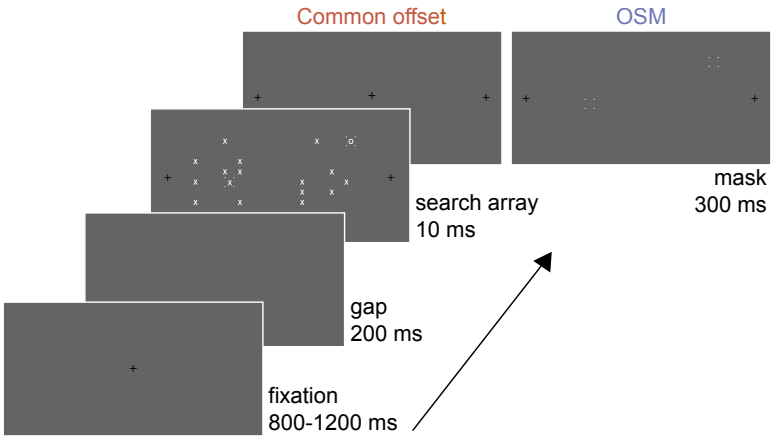

Figure 6: **Schematic overview of the experimental paradigm.** Observers made speeded saccades towards the location of the target (letter "O" surrounded by four dots) or indicated the location of the target with button presses.

4.2.2 Study 2: Fine-grained time course indicates that fastest responses can produce awareness of object

To analyze how this impairment developed over time, we compared the response time distribution obtained under masking to a surrogate condition, which represents the null hypothesis that the mask-induced performance impairment is independent of response time. We found that object substitution masking impaired performance in the saccadic

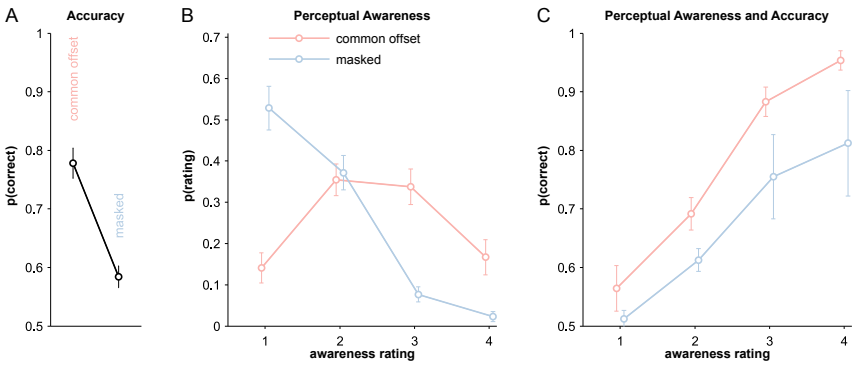

Figure 7: **A** Proportion of correct responses for common offset and masked trials. All error bars represent standard error of the mean. Masking reduced accuracy by approximately 20%. **B** proportion of trials on which participants reported each of the four levels of the perceptual awareness scale. Masking strongly reduced participants' subjective awareness of the target stimulus. **C** proportion of correct responses increased with increasing awareness rating in both conditions.

choice task predominantly for slower saccades (RT<352), while the fastest saccades under masking were as accurate as comparably fast saccades without a mask (Fig. 8A). This finding replicates the results of Crouzet et al. (2014) and indicates that OSM has a dynamic time course and interferes mostly with later processing stages.

An important question is whether successful processing during the early feedforward sweep (as indicated by a correct fast saccade under masking) remains unconscious if the processing is disrupted during later reentrant processing (Lamme, 2006). We addressed this question by comparing fast correct to fast incorrect trials. If the information that triggered fast correct responses had remained unconscious, participants should be equally (un)aware on correct and incorrect trials. By contrast, we found that awareness was reported as higher on fast correct trials than on fast incorrect trial, indicating that participants were well aware of the stimulus if they were correct (Fig. 8B). This finding is consistent with a study by Koivisto (2012) who demonstrated that confidence ratings discriminated between correct rejections on target-absent trials and misses on target-present trials, indicating that some sense of object-presence survived the disruption of the mask. He concluded that elementary conscious perception can be reached in purely feedforward manner. Together, these findings indicate that stimulus information computed during the early feedforward sweep is not principally devoid of consciousness, as some authors have proposed (Lamme, 2006). As previously mentioned, this seemingly conflicting result could be a consequence of less sensitive measures of consciousness in previous experiments. As expected by other theoretical frameworks, different degrees of visual consciousness may relate to different neural correlates (Overgaard and Mogensen, 2014, 2015; Andersen et al., 2015).

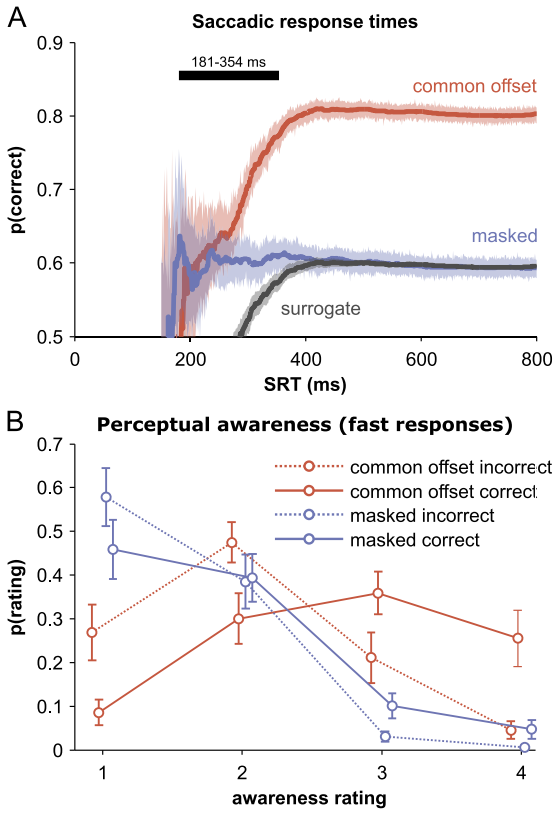

Figure 8: **A** Time course of accuracy obtained from cumulative SRT distributions for correct and incorrect responses pooled across all observers (shaded areas correspond to 95% CI). Accuracy at a given time point (e.g. 300 ms) corresponds to the proportion of correct responses among all SRT at least as fast as this value (e.g. all SRT $\leq$ 300 ms). The horizontal black line on top represents the time points (181–354 ms) at which the observed accuracy time-course under masking was significantly better than predicted by the null hypothesis (surrogate data). Note that the fastest saccades under masking were as accurate as similarly fast saccades without masking. **B** Proportion of trials on which participants reported each of the four levels of the perceptual awareness scale separately for correct and incorrect trials. Only trials with fast saccades are shown. Error bars represent standard error of the mean. Subjective awareness depends strongly on response accuracy, even for fast masked trials.

4.2.3 Study 2: Neural orienting of attention can be triggered during the initial feedforward sweep

A number of studies have investigated neural signatures of target processing under object substitution masking by analyzing the N2pc component of the ERP (Woodman and Luck, 2003; Woodman, 2010; Prime et al., 2011; Harris et al., 2013). The N2pc is thought to reflect the attentional selection of a task-relevant visual stimulus following an attentional shift to the stimulus' location (Eimer, 1996; Busch et al., 2010b,a). These studies demonstrated that object substitution-masked targets elicited an N2pc and thus a shift of spatial attention towards the target, even when the target could not be accurately reported. Woodman and Luck (2003) have interpreted this finding as showing that the shift of attention indicated by the N2pc is triggered during the initial feedforward sweep, before the mask interferes with the representation of the target stimulus. However, previous studies of the N2pc under OSM had participants report target presence (Woodman and Luck, 2003; Prime et al., 2011) or identity (Harris et al., 2013) using delayed manual responses. Without access to informative response times, it is difficult to tell at what time and during which processing stage information about the target stimulus was present and when it was disrupted by the mask. Thus, the question remains whether the N2pc can be triggered during the initial feedforward processing stage. To address this question, we tested how the N2pc was related to response speed. As described above, we found that masked trials with fast saccades (SRT<352 ms) were as accurate as equally fast common offset trials, while slower masked trials were markedly less accurate than equally slow common offset trials. Thus, fast responses can serve as a proxy for trials in which stimulus information was represented in the initial feedforward sweep, and we tested if an N2pc was present on those trials. Indeed, we found an N2pc for correct masked trials *only* for fast, but not for slow responses (Fig. 9). By contrast, we found an N2pc on correct common offset trials regardless of response speed. However, in contrast to previous studies, we found no significant N2pc on incorrect trials, except for a weak "N2pc" for fast common offset trials, but this effect actually had a reversed polarity (i.e. more negative ERP at ipsilateral channels). In fact, the magnitude of the N2pc across conditions was strongly dependent on participants' subjective awareness of the target, such that no N2pc was found when participants reported "no experience" or "weak glimpse".

One important implication of this finding is that in our version of the OSM paradigm, the N2pc indeed reflects processing of the target stimulus. Had the N2pc reflected processes associated with saccade preparation or execution instead, every condition should have shown an N2pc, but the polarity should have been tied to the direction of the saccade.

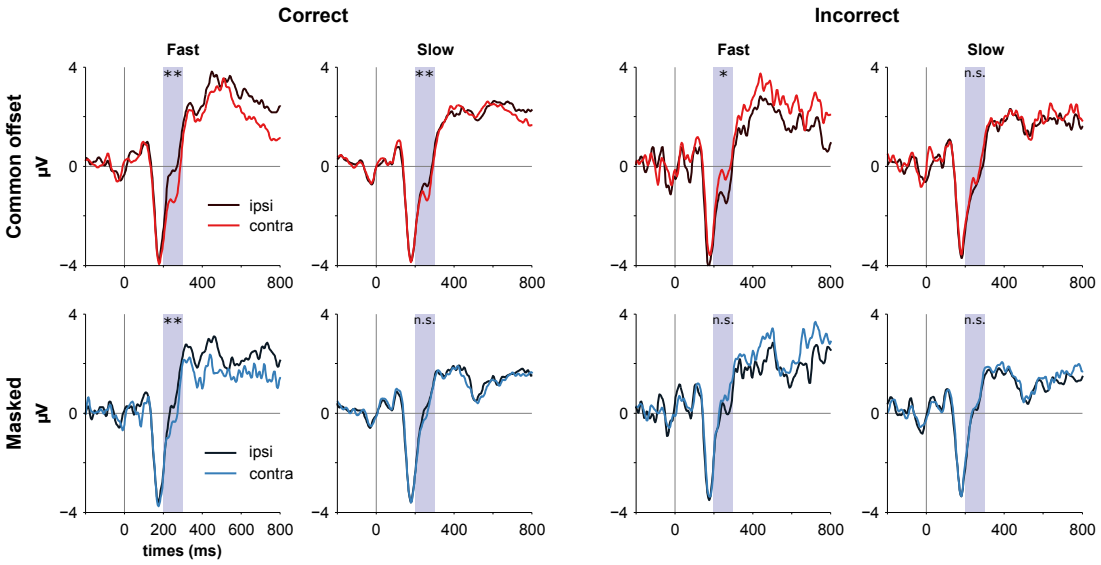

Figure 9: Grand-averaged ERPs shown separately for common offset (top) and masked (bottom) trials. Additionally, panels show ERPs separately for trials with correct and incorrect and with fast and slow responses (i.e. saccades faster/slower 352 ms). N2pc was observed for all correct common offset trials and only for fast correct masked trials.

4.2.4 Study 2: Summary of results

We show that saccades faster than 350 ms can escape the influence of object substitution masking, while slower saccades are associated with reduced accuracy and subjective awareness. On fast trials that seem to escape masking effects, we observe a neural correlate of attentional shifts, N2pc, towards the masked targets. Correct performance on fast masked trials was associated with increased ratings of subjective awareness, indicating that stimulus representations established in this early phase can be conscious.

4.3 Study 3: Fastest responses escape OSM for both manual and saccadic responses

Here, we inspected the time-course of accuracy under OSM using manual and saccadic responses. Our goal was to extend the paradigm to another response modality and establish whether masking affects the accuracy of the fastest *manual* responses. Secondly, we aimed to replicate our previous finding that masking does not impair the accuracy of the fastest saccadic responses (Crouzet et al., 2014). We inspected average accuracy, median and minimum reaction times and conducted a fine-grained analysis of the accuracy-RT relationship using the full distribution of single-trial response times.

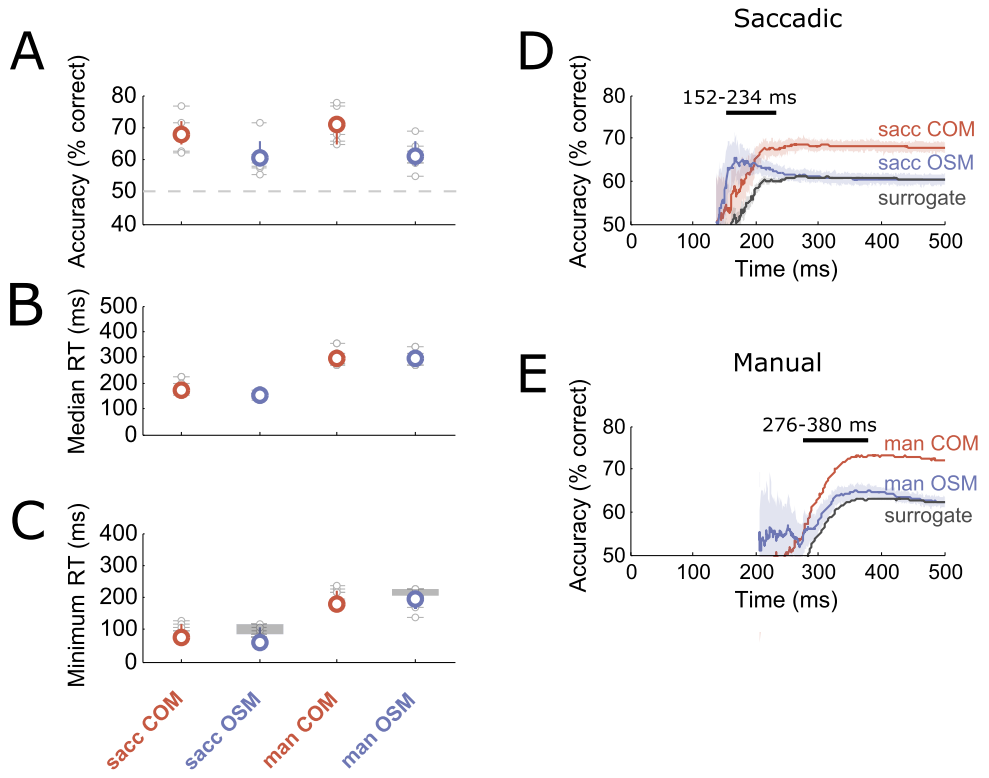

Figure 10: **Accuracy and reaction times (RT) results. A** Accuracy averaged across observers (colored circles) under common offset (red) and masking (blue) in both response conditions with corresponding 95% CI. Light gray circles indicate performance of individual observers. **B** Average and single-observer median RT. Same conventions as in (A). Median RT were comparable in all conditions. **C** Average and single-observer minimum RT, computed as the fastest RT at which accuracy was above chance level. For masked conditions, superimposed light gray areas correspond to the 95% CI of the surrogate condition. Minimum RT for OSM were significantly faster than expected based on the surrogate condition. **D, E** Accuracy time-course, obtained from the cumulative RT distributions for correct and incorrect responses pooled across all observers (shaded areas represent the 95% CI). For better readability, latencies before 130 ms for saccadic and before 200 ms for manual responses are not displayed because not enough data were available to get a reliable measurement of accuracy. Horizontal black lines represent the time points at which the observed accuracy time-course in the masked condition was significantly different from the surrogate time-course (obtained from the same resampling as in (C); non-parametric bootstrap test). Note that the fastest responses under OSM were as accurate as similarly fast responses without masking (red trace) and significantly more accurate than predicted by the surrogate condition (black trace).

Our results validate the earlier finding that response timing is a critical parameter in object-substitution masking. Here we show again that fastest saccadic responses escape masking. Further, we were able to demonstrate this effect in a different response modality (see Figure 10). Our results clearly indicate that early manual presses also escape the effects of OSM. Importantly, this finding is not just an extension of a previous result, but also rules out saccade-specific mechanisms, such as saccadic suppression or saccade-induced retinal shift as potential confounds in our previous finding. First, saccadic suppression is a process that is active already prior to saccade onset and transiently reduces sensitivity in early visual areas to block out the retinal blur (Ross et al., 2001). For early responses, this effect could potentially erase the trailing mask. Second, the shift of the retinal image may cause a spatial misalignment of target and mask in retinotopic coordinates and thus disrupt the spatial promixity of target and mask, which the reentrant model of OSM assumes to be a necessary precondition for masking. Both of these artifacts would render the masking ineffective for fast saccadic responses. The accuracy pattern we observe with manual responses demonstrate that our previous finding can be reproduced in other modalities and therefore does not represent an artifact of such perisaccadic processes. The accuracy time-course for manual responses parallels that for saccadic responses with a delay of about 120 ms. Both this relative difference and the absolute RT values are consistent with the report of Bacon-Macé et al. (2007), who previously compared accuracy and RTs for saccadic and manual responses in a 2AFC discrimination task.

While our findings fit the object-substitution model, it should be noted that equating the accuracy time-course of behavioral responses to stages of the visual processing is somewhat speculative. We cannot be sure that fast and accurate saccades or manual presses are necessarily triggered during the feedforward sweep, whereas slower masked responses correspond to the disruption of reentrant processes. However, other models that do not specifically assume object-substitution, such as the retino-cortical dynamics (RECOD) model, also predict an effect of masking on late feedback processing (Öğmen, 1993; Öğmen et al., 2003). That said, our results inform models of masking by object substitution by showing (a) that the mask impairs processing at a rather late stage and (b) that stimulus information is processed and available for response initiation at an early stage.

4.3.1 Study 3: Summary of results

Next to replicating the previous finding that fast responses escape visual masking, our findings in the manual condition allow us to rule out saccade-specific confounds as well as directly relate our findings to the body of literature that explores masking effects on manual responses.

5 Conclusion

In this series of experiments, we inspected mechanisms of visual perception at three intersections – neural activations that accompany saccade generation to targets (Study 1), behavioral, neural and subjective responses that accompany target detection (Study 2), and responding to target in two different modalities (Study 3). While these experiments were conducted with different methods and tested different theoretical frameworks, their common purpose was to inspect the fine-grained time-course of neural and behavioral events that narrowly precede action. Whether this action was to make a saccade or press a button, our experimental tasks were designed to encourage fast responses, which allowed little time for reorientation or correction. This is a highly artificial situation, as in the real world, objects around us rarely disappear after a few milliseconds. However, this manipulation allowed us to capture the initial responses of the visual system. Naturally, our data may also reflect the errors that the visual system makes when forced to perform under pressure. Therefore, in all studies we included surrogate conditions that represented the null hypothesis. These surrogate data were designed to imitate real data with maximal precision (such as reaction times or accuracy), but not contain the event of experimental interest (interaction of probe and saccade, masking). This methodological step allowed us not only to compare, but also to validate the findings in our experimental conditions. In sum, this work has contributed innovative approaches to recording and correcting data containing large eye movements with EEG, which was previously avoided due to heavy artifacts. Theoretical impact of this work includes: identifying correlates of attention and suppression in human EEG, which will inform future studies employing similar methods; contributing empirical insights that will further inform the theory of object substitution masking.

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6 Eidesstattliche Erklärung

Ich erkläre, dass ich die vorliegende Arbeit selbstständig und nur unter Verwendung der angegebenen Literatur und Hilfsmittel angefertigt habe;

dass ich die Doktorarbeit an keiner anderen Universität eingereicht habe und keinen Doktorgrad in dem Promotionsfach Psychologie besitze;

und dass mir die zugrunde liegende Promotionsordnung der Mathematisch - Naturwissenschaftlichen Fakultät II (Name geändert zur Lebenswissenschaftlichen Fakultät) vom 17.01.2005, zuletzt geändert am 1.02.2006, veröffentlicht im Amtlichen Mitteilungsblatt der HU Nr. 34/2006, bekannt ist.

Berlin, den 29. September 2015

Lyudmyla Y. Kovalenko